ART. 14. LATE PLEISTOCENE RECORDS OF THE YELLOW-CHEEKED VOLE, *MICROTUS XANTHOGNATHUS* (Leach)

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The yellow-cheeked vole, *Microtus xanthognathus* (Leach), has been reported from numerous, widely scattered localities in the subarctic of western North America, from about 52° N. latitude in Alberta, north to the Mackenzie River delta, and from the Kuskokwim River in western Alaska, east to Fort Churchill and the Nelson River in Manitoba. It is apparently very local in distribution and is not often taken by collectors.

This is one of the largest species in the genus *Microtus* closely approaching the size of the water vole, *Microtus richardsoni* (DeKay). It is a colonial animal, an extensive burrower, and one of the rarest North American microtines.

Skeletal remains referred to this species have been recovered from two Late Pleistocene cave deposits in the Appalachian Mountain region, one in south-central Pennsylvania and the other in west-central Virginia. These constitute the first record of the animal from the Pleistocene of eastern North America. (Fig. 1.)

An additional Pleistocene record may be a specimen recovered from permafrost deposits at Chicken, Alaska. The specimen, a mummy with hair, is in the American Museum of Natural History. In the opinion of the collector, O. W. Geist, who noted several deposits of vivienite on it, the specimen is a true fossil. We wish to thank Dr. Richard G. Van Gelder for calling our attention to this specimen.

The first site to yield remains of this mouse was Natural Chimneys, Mt. Solon, Augusta County, Virginia, 38° 20′ N. lat., 79° 5′ W. long., alt. 1500 feet, Stanton Quadrangle, Va.-W.Va. U. S. Geological Survey topographical map, 1894 edition. The Natural Chimneys, located on the western side of the Shenandoah Valley, are a group of natural limestone pillars with a shallow cave at their base. The pillars seem to be erosion remnants of a former fissure system. Bones and teeth were recovered from several spots in the floor and walls of the cave by Ted B. Ruhoff and later by Carnegie Museum field parties under the direction of J. LeRoy Kay. Within historic times a stream flowed about the base of the "chimneys," and the bone-bearing deposit may have been reworked by water since its initial deposition. The fauna is probably derived from several time periods but none is believed older than late Pleistocene. The collection is unstudied but contains at least the following forms: *Condylura, Scalopus, Sorex, Microsorex, Blarina, Cryptotis, Myotis, Eptesicus, Pipistrellus, Mephitis, Mustela, Lynx, Ursus, Marmota, Tamias, Glaucomys, Sciurus, Tamiasciurus, Neotoma, Peromyscus, Synaptomys, (Mictomys), Phenacomys, Clethrionomys, Microtus, Pitymys, Ondatra, Castor, Castoroides, Zapus, Napaeozapus, Lepus, Odocoileus* ?, *Mylohyus* ?, plus fragments of birds, snakes (including a large *Crotalus* near *adamanteus* vertebra), amphibians and fish. All material is fragmentary. The *Castoroides*, one upper molar, was discovered by Mr. Ruhoff. Six specimens collected by the Carnegie Museum field parties were identified as *Microtus cf. xanthognathus* (Leach). These include two broken right mandibles containing the

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first two molars, 1 broken left mandible with m1-m2, 1 broken left mandible containing the stumps of m1-m2, 1 left maxilla with complete dentition and 1 palate with M1-M2 on both sides, all catalogued under C.M. 5861.

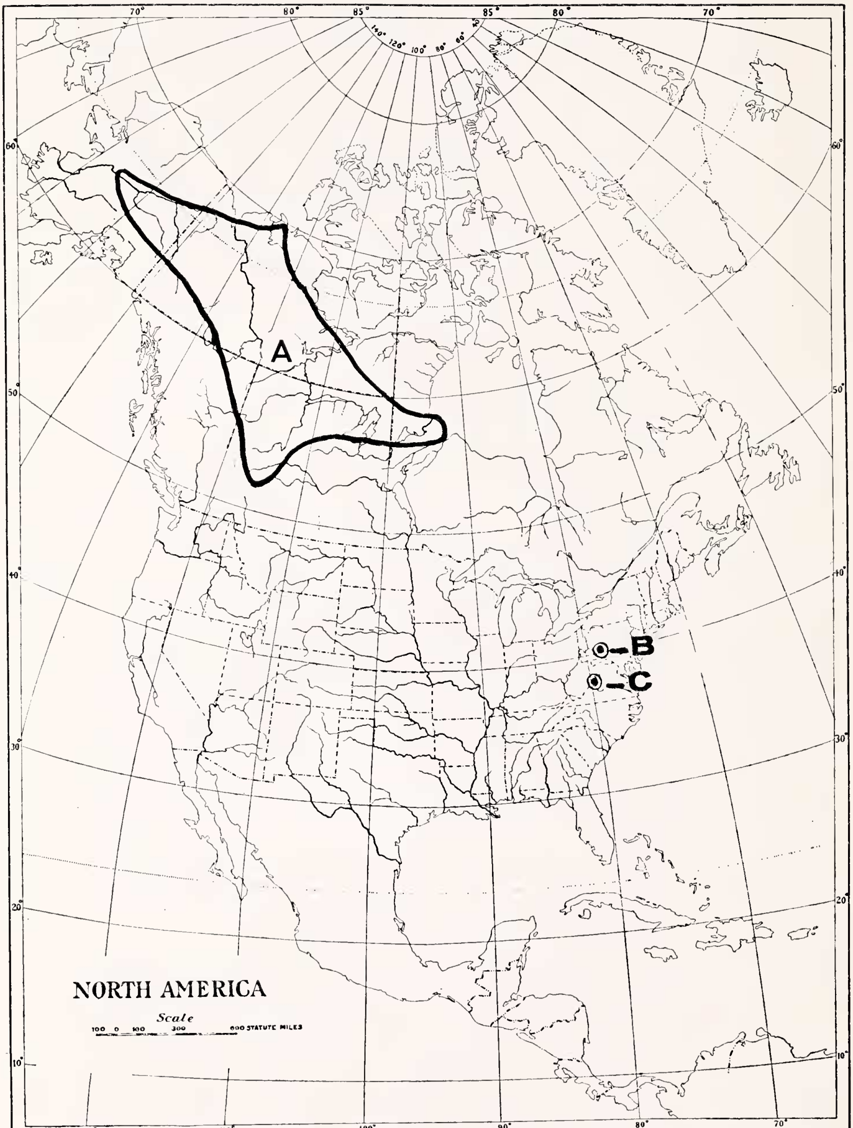

Fig. 1. Outline map of North America. A. Present range of *Microtus xanthognathus* (Leach). (Modified from Hall & Kelson, 1959.) B. Lloyd's Rock Hole, New Paris, Bedford County, Pennsylvania. C. Natural Chimneys, Mt. Solon, Augusta County, Virginia

The second locality is "Lloyd's Rock Hole" or Sink-hole no. 4, 1½ miles northeast of New Paris, Bedford County, Pennsylvania, 40° 7′ N. lat., 78° 37′ W. long., alt. 1500 feet. Bedford Quadrangle, U. S. Geological Survey, 1908 edition. This highly fossiliferous fissure deposit was discovered in the spring of 1958 by Carnegie Museum and National Speleological Society field parties composed of Rita Battistoli, Ralph C. Bossart, Gerald W. Frederick, Roscoe Hall, Harold Hamilton, Beverly Hofecker, J. LeRoy Kay, John A. Leppla, Allen D. McCrady, and other members of the Pittsburgh Grotto of the N. S. S.

Excavation is not complete at this writing but the fauna contains at least the following mammalian forms: *Condylura, Parascalops, Sorex, Microsorex, Blarina, Myotis, Eptesicus, Pipistrellus, Martes, Mustela, Marmota, Tamias, Tamiasciurus, Glaucomys, Neotoma, Peromyscus, Synaptomys, (Mictomys), Phenacomys, Microtus, Pitymys, Clethrionomys, Zapus, Napaeozapus, Erethizon, Mylohyus,* and *Odocoileus* ?. The material is both abundant and well preserved. The entire fauna appears to have been contemporaneous with possible intrusions of a few modern burrowing forms. Pollen analysis of the clay matrix by Paul S. Martin, Geochronology Laboratories, University of Arizona, indicates a boreal, pine-dominant forest cover.* This fauna is currently under study and will form the topic of a future paper.

Microtus xanthognathus (Leach) was the second most common microtine in the deposit, exceeded only by *Clethrionomys* cf. *gapperi* (Vigors). Remains referred to the yellow-cheeked vole include, to date, 21 partial skulls, 24 right mandibles, 23 left mandibles, and 42 additional bones representing most of the major skeletal elements. Remains of this mouse occurred throughout the excavation from four feet beneath the surface to the present excavation level some 20 feet beneath the mouth of the sink-hole. It was apparently in temporal association with *Microtus pennsylvanicus* (Ord) and *Microtus chrotorrhinus* (Miller) both of which are represented by well preserved skulls and mandibles.

A comparative study of the New Paris fossil *M. xanthognathus* material and modern crania of various ages and localities was made. Results are presented below.

The authors wish to thank Dr. J. Kenneth Doutt, Dr. Claude L. Hibbard, and Dr. J. LeRoy Kay for much valuable advice and assistance; the members of the Pittsburgh Grotto, National Speleological Society for their unstinting work on the New Paris excavations; John A. Leppla for the photography, Harry K. Clench and Dr. Wendell P. Rand for mathematical assistance and advice; and Caroline A. Heppenstall, Alice M. Guilday and Patricia M. Guilday for editing, clerical assistance and art work. We would also like to thank the following people who loaned us specimens under their care: Dr. Barbara Lawrence, Museum of Comparative Zoology at Harvard; Dr. Richard G. Van Gelder, American Museum of Natural History; Dr. David H. Johnson, United States National Museum; Dr. Austin W. Cameron, Canadian National Museum; Dr. L. J. Rowinski, University of Alaska Museum. We also wish to thank the two men who, by their co-operation and generosity, were most responsible for this project's existence, Mr. Gordon E. Brown, owner of Natural Chimneys, Mt. Solon, Virginia, and Mr. Oscar Miller of

* A radiocarbon date of 11,300 ±1000 years run on carbon particles (forest fires?) in the matrix has just been received from Yale University Geochronometric Laboratory.

New Paris, Pennsylvania, owner of Lloyd's Rock Hole. Excavations at the latter site are being financed by a grant from the A. W. Mellon Educational and Charitable Trust, and conducted by field parties from Pittsburgh Grotto, National Speleological Society and Carnegie Museum.

All measurements of 10 mm. or less were taken with an ocular micrometer at a magnification of 10×. Larger measurements were taken to the nearest 0.5 mm. with an E. G. Bogush measuring scale. All camera lucida renderings by one of us (Bender) and dental studies were done at 10× under a dissecting microscope.

Dental Variation

Variation in gross size, due to age, is especially great in those microtines whose molars continue to grow throughout the life span of the animal. In a sample of 30 modern skulls of *M. xanthognathus* from various localities (12 immature, but with the molars erupted and the occlusal pattern established, and 18 adults), the alveolar length of the upper tooth-row varied from 6.0 mm. to 9.1 mm., an increase of 3.1 mm. or 34% from youngest to oldest. The occlusal length of M1 varied from 2.0 mm. to 3.0 mm., a gain of 33⅓%.

Once a functional triturating surface has been established early in the life of the animal, there is no change in the occlusal patterns of the individual molars. Wear does take place, but since the molars are compensating for this by elongation, and the occluding surface of each molar is a plane, tooth-wear does not express itself in any way that can be followed. It is, therefore, often impossible to tell, from isolated molars alone, whether a given specimen is from an adult of a *smaller* species such as *M. pennsylvanicus* or an immature individual of a *larger* species such as *M. xanthognathus*. In many cases this is true of isolated mandibles with complete dentitions (although the occlusal patterns of m1 and m3 are *usually* diagnostic). This is no great problem when age changes in the skull can be examined or when dealing with modern material; but as much fossil material is fragmentary and scanty, gross measurements of individual molars may be of little significance when considered alone.

Each upper incisor of *M. xanthognathus* bears a shallow, longitudinal groove on its anterior face. This is very apparent on adult specimens but is not noticeable on smaller, immature animals. Grooving was noted on the upper incisors of the fossil New Paris material exactly as in modern specimens. In profile, the incisors of the New Paris fossil population (Fig. 2) appear more pro-odont than their modern equivalents. Their tips appear less recurved, but the degree of curvature of the incisor appears to be the same in both samples. This difference is mechanical in origin rather than genetic, due to "settling" of the fossil incisors in their sockets. The maxilla of a fresh *Microtus pennsylvanicus* (Ord) was dissected and the developing root of the incisor examined. In a fresh specimen the developing bulb of the incisor normally sits on the floor of the maxilla immediately anterior to the alveolus of the first upper molar. But as the skull dries and tissues shrink, a hollow area, about as deep as the width of the incisor, is left between the back of the incisor and the wall of the maxilla. This same area was examined in a fossil *M. xanthognathus* skull (C.M. 5571). In this case the delicate posterior rim of the incisor was crushed down again the maxilla. The space that originally housed the soft tissues of the developing tooth was eliminated and it was quite obvious that the incisor had been pushed towards the rear. As

Fig. 2. Pseudo-procumbent incisors of fossil *Microtus xanthognathus* (Leach) due to post-mortem alveolar settling

Modern	*Fossil*
M.C.Z. 5584	C.M. 5556
M.C.Z 5585	C.M. 5559
U.A. 1871	C.M. 5553

each incisor is a segment of a circle any displacement backwards would make the tips appear to migrate forwards, and hence be more pro-odont in profile. This same condition is often noted in modern skulls that have been macerated and the incisors subjected to any pressures. This displacement was also noticed in many of the lower jaws as well as in rodent skulls of other species from Lloyd's Rock Hole.

There is a considerable amount of individual variation in the molar teeth of *M. xanthognathus.* The thickness of the enamel band, as seen from the occlusal surface, increases, apparently with age. Salient angles and re-entrant valleys may vary from broad and U-shaped (C.M. 5585, Fig. 4), to sharp and acute (C.M. 5572, Fig. 4). Individual alternating triangles of the molars may be broad or narrow and their exact configurations are highly variable. The *pattern* of the occlusal surface of the molars remains fairly constant; that is, it varies within definite limits. Lower molars are more variable than the uppers.

Upper first molar. Normal pattern is an anterior crescent followed by two alternating triangles and a posterior crescent. Of the 28 modern and 13 fossil skulls examined but one variant was noted. A modern specimen (U.A. 10, Fig. 3) had the anterior crescent of the left M1 nearly divided in half

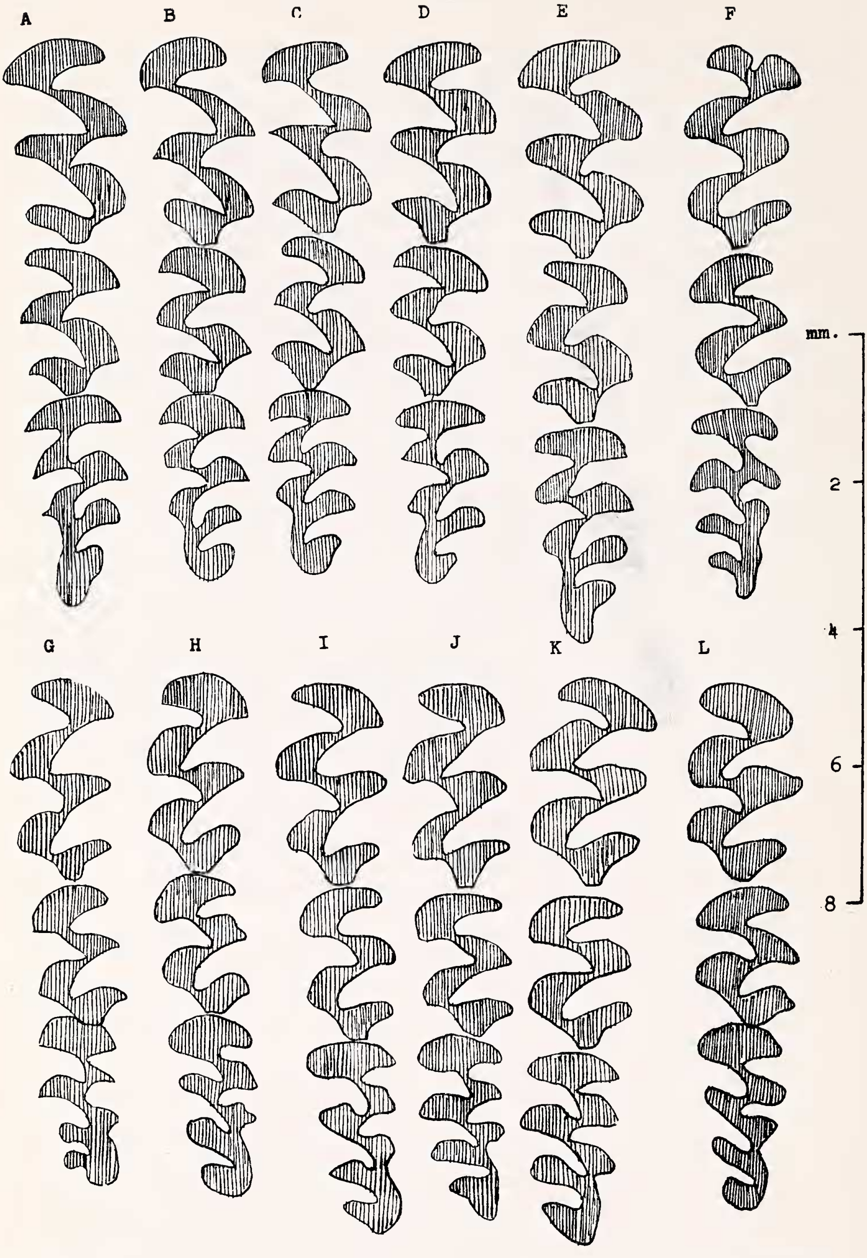

Fig. 3. Occlusal patterns of upper molars of *Microtus xanthognathus* (Leach)

A. C.M. 5554 Right M1-M3 fossil
B. C.M. 5555 Right M1-M3 fossil
C. C.M. 5556 Right M1-M3 fossil
D. C.M. 5562 Right M1-M3 fossil
E. U.S.N.M. 7702 Right M1-M3 recent
F. U.A. 10 Left M1-M3 recent
G. C.M. 5578 Left M1-M3 fossil
H. C.M. 5557 Left M1-M3 fossil
I. C.M. 5558 Left M1-M3 fossil
J. C.M. 5577 Left M1-M3 fossil
K. A.M.N.H. 16006 Left M1-M3 recent
L. C.M. 5557 Left M1-M3 fossil

by an anomalous medium anterior re-entrant valley. This valley was filled with cement and lined with unbroken enamel. The right M1 was normal.

Upper second molar. Normal pattern is an anterior crescent followed by two alternating triangles and posterior crescent. No variation was noted in

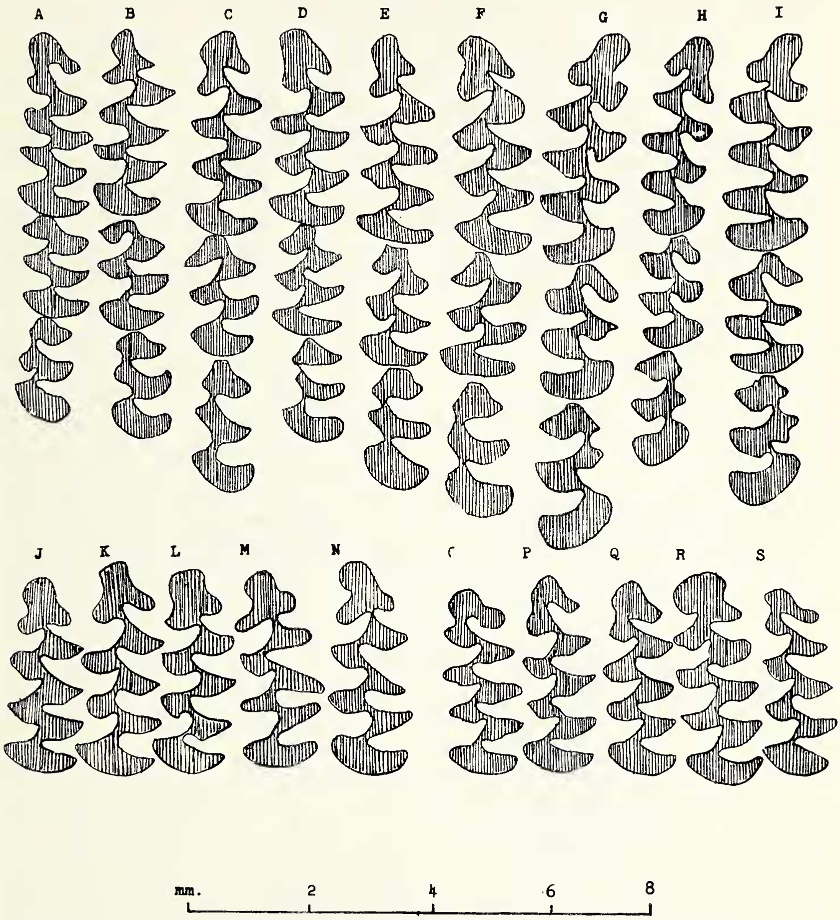

Fig. 4. Occlusal patterns of lower molars of *Microtus xanthognathus* (Leach)

A. C.M. 5540 Left m1-m3 fossil
B. C.M. 5541 Left m1-m3 fossil
C. C.M. 5572 Left m1-m3 fossil
D. C.M. 5582 Left m1-m3 fossil
E. U.S.N.M. 128330 m1-m3 recent
F. U.S.N.M. 271710 m1-m3 recent
G. C.M. 5583 Right m1-m3 fossil
H. C.M. 5589 Right m1-m3 fossil
I. A.M.N.H. 16006 Right m1-m3 recent
J. C.M. 5543 Left m1 fossil
K. C.M. 5562 Left m1 fossil
L. C.M. 5564 Left m1 fossil
M. C.M. 5566 Left m1 fossil
N. C.M. 5566a Left m1 fossil
O. C.M. 5581 Left m1 fossil
P. C.M. 5584 Left m1 fossil
Q. C.M. 5585 Left m1 fossil
R. C.M. 5586 Left m1 fossil
S. C.M. 5590 Left m1 fossil

28 modern and 13 fossil dentitions.

Upper third molar. Highly variable. Normal pattern is an anterior crescent followed by three alternating triangles and a posterior, lingually directed loop composed of two lingually directed "arms" which are confluent buccally. The third alternating triangle may or may not be confluent with the posterior loop, but it usually is. An incipient fourth salient angle may be present on the buccal side of the tooth (C.M. 5561), or it may be completely absent. It was present in four out of 28 modern and 1 out of 12 fossil examples. An incipient lobe, rarely well developed, may be present at the back of the posterior lobe (C.M. 5554, Fig. 3). An incipient fourth lingual re-entrant is rarely present, but in one modern (U.A. 10, Fig. 3) and one fossil dentition (C.M. 5578, Fig. 3) the fourth lingual re-entrant had split the posterior lobe into two sub-lobes. The incipient posterior lobe was noted in 8 out of 28 modern dentitions, and 4 out of 10 of the New Paris fossils. One fossil specimen (C.M. 5557, Fig. 3) was unique in that the third lingual re-entrant valley extended clear across the tooth, isolating its posterior lobe.

First lower molar. Normal pattern is a posterior triangle, five isolated alternating triangles and an anterior trefoil. This tooth, especially its anterior end, is highly variable, and no two, modern or fossil, were quite alike. The anterior lobe of the trefoil may be blunt and bulb-shaped (C.M. 5584, Fig. 4) or attenuated and directed antero-laterally (C.M. 5583, Fig. 4). The posterior lobes of the trefoil (the 5th lingual and the 4th buccal salients) may be blunt or sharp, aborted or robust. The anterior re-entrants of the trefoil may be present (C.M. 5586, Fig. 4) or absent (C.M. 5582, Fig. 4), and are usually quite shallow. Rarely the fifth alternating triangle is broadly confluent with the anterior trefoil. One fossil specimen was unique (C.M. 5540, Fig. 4); the first and second alternating triangles had united into a crescent, and all triangles and crescents were narrowly confluent with one another. Rarely (C.M. 5566a, Fig. 4) the fourth lingual re-entrant valley meets the third buccal re-entrant valley, a condition more typical of *M. pennsylvanicus*. Normally (C.M. 5572, Fig. 4) the fourth lingual re-entrant turns forward and penetrates the base of the trefoil.

There were so many intermediate variations present in the anterior part of m1 that they could not be classified into particular varieties. No variations were observed in the modern dentitions, however, that could not be matched, or nearly so, with fossil specimens from New Paris or Mt. Solon.

Second lower molar. Normal pattern is a posterior crescent, two alternating triangles and an anterior buccally-directed lobe. The basic pattern does not vary, but the degree of isolation of the triangles does to a limited extent. They may be completely isolated from one another and from the posterior crescent and the anterior lobe (U.S.N.M. 271710, Fig. 4), or confluent (C.M. 5540, Fig. 4). The anterior lobe varies in shape from triangular (C.M. 5572, Fig. 4) to vermiform (C.M. 5589, Fig. 4), this was noted in both modern and fossil specimens.

Third lower molar. The third lower molar is a highly variable tooth and can hardly be said to have a "normal" pattern. Three types of occlusal patterns were noted. (Fig. 5). 1. A posterior crescent, two widely confluent alternating triangles and an anterior cresent (C.M. 5583, Fig. 4). 2. A posterior crescent, two isolated alternating triangles and an anterior crescent.

3. The two alternating triangles are completely confluent resulting in an occlusal pattern of three crescents (C.M. 5589, Fig. 4).

	New Paris fossil. Sample size, 8 number	percentage	Modern. Sample size, 25 number	percentage
Type 1	3	38%	10	40%
Type 2	2	25%	5	20%
Type 3	3	38%	10	40%

Fig. 5. Chart showing frequency of dental variations in the lower third molar of *Microtus xanthognathus* (Leach)

Cranial Variation

The fossil skulls from New Paris average slightly smaller in most dimensions, particularly in the rostral area, than the modern material we have examined. Fortunately the fossils are so well preserved that their individual ages may be estimated. Age criteria used were: degree of development of the interorbital crest, presence or absence of frontal pit, and general rugosity of the skull. Evidence of Haversian canal activity, indicating active bone deposition was noted on the dorsal surface of the zygomatic arms of the maxilla.

The fossil series was judged to be almost entirely composed of young, actively growing animals, probably sexually mature but not yet fully grown. Only one specimen (C.M. 5576) is believed to be from a fully adult animal. As a result it is hard to obtain modern comparative material of a comparable age level (and growth changes in *M. xanthognathus* are so extreme that this is a necessity). The apparent scarcity of the young adult age class in the modern material, and its almost universal presence in the fossil collection is probably because a sink-hole trap does not operate at random throughout a population. There is a greater probability that young animals, rather than older established ones, will be trapped. The amount of random wandering, hence the chances of blundering into a sink-hole, would be greatest among the younger, unestablished animals. Modern specimens are collected primarily by trapping. A mousetrap is somewhat less selective than a sink-hole, producing a greater age spectrum in any given collection. And since modern collections of this animal are rather small and growth changes so pronounced, any conclusions arrived at without making due allowance for age are apt to be spurious. We have interpreted the slightly smaller average measurements of the fossil crania as being primarily due to the biased age composition of the sink-hole trapped collection, rather than to any genetic difference between the two populations—fossil and modern. The extent of these genetic differences, if they existed, was apparently not expressed in the skeleton or the dentition, as preserved in the cave material. We are unable to find any consistent morphological differences between the fossil and the modern populations of *Microtus xanthognathus* (Leach) in the material examined by us.

This close similarity between the modern form and its late Pleistocene Pennsylvania counterpart is, we believe, due to the lack of any significant degree of geographical isolation or of ecological change that may have stimulated evolutionary selection. Admittedly we have considered only the skull and the dentition of the animals involved, but, based upon the evidence at hand, plus the boreal forest affinity of the associated fauna at New Paris, the Pennsylvania record, and by inference the Virginia one as well, is indicative of a former cooler time in the area. The present range of the yellow-cheeked vole, therefore, represents but a remnant of an earlier maximum glacial extension south to at least 37° N. latitude in the Appalachian region. It has, apparently migrated to the north, during post-Wisconsin times, keeping pace with climatic changes.

As both *Microtus xanthognathus* and *Microtus chrotorrhinus* occurred together in the Lloyd's Rock Hole local fauna, with no trace of intergradation in the dentition or the crania, this would seem to argue for the validity of the two species (See Hall and Kelson, 1959, p. vi of v. 1 and p. 741 for discussion of this point). The interesting question then presents itself of why *M. xanthognathus* should be restricted today to the western half of the Hudsonian life zone, while *M. chrotorrhinus* appears to be restricted to the eastern half, plus a relict distribution down the Appalachians. The two have been distinct forms since at least the Late Pleistocene. They occurred together in the Appalachians at one time. Yet they do not occupy common ground today. More research must be done on the present habitat requirements of these voles and on Late Pleistocene fauna from the area before this question can be answered.

SUMMARY

Skeletal remains identified as *Microtus xanthognathus* (Leach) have been recovered from Late Pleistocene cave deposits at Natural Chimneys, Mt. Solon, Augusta County, Virginia and at Lloyd's Rock Hole, New Paris, Bedford County, Pennsylvania. This constitutes a range extension of about 1400 miles in aerial distance and 14 degrees of latitude. The present range of this vole is from Alaska to Manitoba, south to about latitude 52 degrees north.

Dental variation in *Microtus xanthognathus* (Leach) is discussed and illustrated.

Microtus xanthognathus (Leach), and *Microtus chrotorrhinus* (Miller) occurred in apparent temporal association in the Lloyd's Rock Hole local fauna, Bedford County, Pennsylvania, during Late Pleistocene times.

REFERENCE

Hall, E. Raymond, and Keith R. Kelson

1959. Mammals of North America. Ronald Press Company, New York. v. 1, p. 1-546; v. 2, p. 547-1083.

LIST OF SPECIMENS EXAMINED

Skulls and skeletal material as follows

ALASKA

Yukon River: A.M.N.H. 16004.

Yukon River, mouth of Porcupine River: A.M.N.H. 16006, A.M.N.H. 16010, M.C.Z. 1593, M.C.Z. 5403, M.C.Z. 5307, M.C.Z. 5308.

Yukon River, 200 miles southwest of Porcupine River: M.C.Z. 1601, M.C.Z. 5302, A.M.N.H. 16009, M.C.Z. 5584, M.C.Z. 5585.

Yukon River, Charlie Creek: U.S.N.M. 128330.

Takotna: U.S.N.M. 271710.

500 miles up the Kuskokwin [*sic*] River: M.C.Z. 17001.

Castle Rocks, 63° 40′ N., 152° 07′ W.: U.A. 9, U.A. 10, U.A. 11, U.A. 12,

Headwaters of Indian Creek, 64° 35′ N., 144° 55′ W.: U.A. 1871, U.A. 1873, U.A. 1875, U.A. 2820, U.A. 2779, U.A. 1872, U.A. 1867.

NORTHWEST TERRITORIES, CANADA

Fort Anderson, Mackenzie River: M.C.Z. 5590.

Fort Resolution, Great Slave Lake: U.S.N.M. 7702.

Peel's River, Mackenzie River: M.C.Z. 5589.

Mackenzie River, 30 miles up Willow River: N.M.C. 4715.

ALBERTA, CANADA

Peace Point, Peace River: M.C.Z. 18894, M.C.Z. 18896, M.C.Z. 18897, M.C.Z. 18939.

NATURAL CHIMNEYS, MT. SOLON, AUGUSTA COUNTY, VIRGINIA

Late Pleistocene: C.M. 5861.

NEW PARIS, SINK-HOLE #4, NEW PARIS, BEDFORD COUNTY, PENNSYLVANIA

Late Pleistocene: C.M. 5534-5544, 5546, 5547, 5550, 5553-5562, 5566, 5570, 5571, 5573, 5576, 5578, 5584, 5589.

Definition of Measurements

Cranial:

1. Length of nasal bones.
2. Greatest width of nasal bones.
3. Least interorbital breadth.
4. Least rostral breadth, taken immediately anterior to the zygomatic plate of the maxillas, and above the incisor swellings.
5. Length of incisive foramina.
6. Transverse width of single upper incisor, taken just back of occlusal surface.
7. Alveolar length of upper tooth row, M1-M3.
8. Occlusal length, M1
9. Occlusal width, M1.
10. Occlusal length, M2.
11. Occlusal width, M2.
12. Occlusal length, M3.
13. Occlusal width, M3.
14. Greatest width across skull, taken at the maxilla-jugal sutures.

Mandibular:

1. Total length of mandible, from most anterior point of symphysis to most posterior point on the angular process.
2. Depth of mandible, from the most anterior point of the alveolus of m1, project the angle of that tooth through the bottom of mandible. (Hard to take with any degree of consistency.)
3. Diastema, from margin of alveolus of incisor to anterior margin of of the alveolus of m1. (Also hard to take consistently.)
4. Alveolar length of lower tooth row, m1-m3.
5. Occlusal length, m1.
6. Occlusal width, m1.
7. Occlusal length, m2.
8. Occlusal width, m2.
9. Occlusal length, m3.
10. Occlusal width, m3.
11. Transverse width of lower incisor.

All measurements are given in millimeters.

Cranial Measurements—*Microtus xanthognathus* (Leach)
New Paris fossil—unaged

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
5558 C.M.	—	—	—	—	—	—	7.7	2.8	1.2	1.9	1.0	2.5	1.2	—
5566 C.M.	—	—	—	—	—	1.3	—	—	—	—	—	—	—	—
5570 C.M.	—	—	—	—	—	—	—	2.7	1.2	1.9	1.1	—	—	—
5579 C.M.	—	—	—	—	—	—	—	2.8	1.2	1.9	1.1	—	—	—
5584 C.M.	—	—	—	—	—	—	—	—	—	1.9	1.2	—	—	—
5585 C.M.	—	—	—	—	—	—	7.4	—	—	—	—	—	—	—
average	—	—	—	—	—	1.3	7.5	2.8	1.2	1.9	1.1	2.5	1.2	—

Mt. Solon, Virginia fossil—unaged

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
5861a C.M.	—	—	—	—	—	—	—	2.9	1.3	2.2	1.2	2.6	1.2	—
5861b C.M.	—	—	—	—	—	—	—	—	—	2.1	1.2	—	—	—

Cranial Measurements—*Microtus xanthognathus* (Leach)
Modern—immature

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
18896 M.C.Z.	7.5	3.1	3.6	3.3	5.8	1.3	7.0	2.4	1.2	1.7	1.2	2.1	.9	16.0
18897 M.C.Z.	7.5	3.0	3.5	3.0	5.7	1.3	6.7	2.5	1.0	1.7	1.0	2.0	1.0	15.5
18939 M.C.Z.	7.3	2.9	3.6	3.1	5.8	1.2	7.1	2.5	1.1	1.8	1.2	2.2	1.2	15.5
5589 M.C.Z.	8.9	2.6	3.4	3.3	6.1	1.3	7.6	2.6	1.1	1.9	1.1	2.7	1.2	17.5
5590 M.C.Z.	8.2	3.3	3.5	3.5	5.4	1.5	7.4	2.5	1.1	1.9	1.1	2.5	1.0	17.0
4715 C.N.M.	—	—	4.0	3.4	6.0	1.2	7.2	2.3	1.2	1.8	1.0	2.3	1.3	—
1811 U.A.	8.4	3.6	3.4	2.9	6.0	—	7.6	2.7	1.2	2.0	1.2	2.7	1.2	18.2
1867 U.A.	—	—	3.6	3.1	4.2	.8	6.0	2.2	1.2	1.9	1.0	1.8	.6	—
1872 U.A.	6.9	3.2	3.8	3.3	5.1	1.1	6.9	2.3	1.0	1.7	.9	2.2	.8	15.5
1873 U.A.	6.0	3.1	3.3	3.2	4.6	—	6.5	2.2	.9	1.8	.8	1.7	.8	13.0
2779 U.A.	5.9	2.8	3.2	3.0	4.6	1.0	6.1	2.0	.9	1.7	.8	1.7	.9	13.5
2820 U.A.	5.6	2.8	2.6	2.6	4.1	—	6.0	2.2	.9	1.5	1.0	1.7	.8	13.5
average	7.2	3.1	3.5	3.1	5.3	1.2	6.8	2.4	1.1	1.8	1.0	2.1	1.0	15.5

Cranial Measurements. Continued

New Paris fossil—immature

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
5556 C.M.	8.7	3.4	3.9	3.6	6.0	1.2	7.7	2.7	1.2	2.2	1.0	2.3	1.2	—
5561 C.M.	—	—	3.9	3.8	6.1	—	7.7	2.7	1.1	1.9	1.1	2.6	1.0	17.0
5573 C.M.	—	—	—	—	5.8	1.2	—	2.5	1.2	1.8	1.1	—	—	—
5578 C.M.	—	—	3.7	3.6	6.0	1.4	7.4	2.8	1.1	1.9	1.1	2.3	1.2	—
average	8.7	3.4	3.8	3.7	6.0	1.3	7.6	2.7	1.2	2.0	1.1	2.4	1.1	17.0

Cranial Measurements—*Microtus xanthognathus* (Leach)
Modern—adult

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
9 U.A.	10.0	4.2	3.8	3.8	7.5	1.7	8.2	2.9	1.2	2.0	1.2	2.7	1.2	20.5
10 U.A.	9.0	3.6	3.8	3.8	6.5	1.7	8.3	2.8	1.3	2.1	1.1	2.5	1.2	19.5
11 U.A.	9.6	3.8	3.6	3.3	7.0	—	8.3	3.0	1.3	2.1	1.2	2.7	1.2	20.0
12 U.A.	9.8	4.0	3.8	3.6	7.3	—	8.4	2.9	1.2	2.1	1.3	2.8	1.3	20.0
16004 A.M.N.H.	9.0	3.6	3.9	3.6	6.4	1.4	8.2	2.8	1.3	2.1	1.2	2.8	1.2	19.5
16006 A.M.N.H.	9.2	3.5	3.5	3.5	6.5	—	8.5	3.1	1.3	2.2	1.3	2.6	1.2	19.5
7702 U.S.N.M.	10.1	3.6	3.8	3.8	7.3	1.7	8.6	3.0	—	2.3	—	2.9	—	20.5
128330 U.S.N.M.	9.6	3.6	3.6	3.6	6.7	1.6	7.8	2.7	1.4	2.3	1.3	2.6	1.3	19.5
271710 U.S.N.M.	10.1	4.3	3.8	3.6	6.7	1.9	8.6	3.2	—	2.3	—	2.9	—	21.0
5302 M.C.Z.	9.4	4.1	3.9	3.5	6.5	—	8.2	2.9	1.2	2.2	1.3	2.7	1.3	—
5304 M.C.Z.	10.0	3.8	—	—	6.7	—	8.1	2.8	1.2	2.1	1.2	2.4	1.2	—
5307 M.C.Z.	8.2	3.6	3.2	3.4	6.2	—	7.6	2.7	1.2	2.0	1.1	2.6	1.2	17.5
5308 M.C.Z.	10.0	3.8	—	2.6	7.2	—	—	3.0	1.1	2.3	1.2	—	—	20.0
5584 M.C.Z.	8.6	3.5	3.8	3.4	6.2	—	7.9	2.7	1.2	2.1	1.2	2.5	1.2	18.5
5585 M.C.Z.	8.8	3.6	3.8	3.8	6.3	—	8.0	2.7	1.2	2.0	1.2	2.7	1.2	19.5
1593 M.C.Z.	9.5	3.6	3.3	3.6	7.1	—	8.2	3.0	1.2	2.1	1.2	2.5	1.2	19.5
1601 M.C.Z.	9.9	3.6	3.5	3.5	6.5	1.4	8.1	2.7	1.2	2.1	1.1	2.5	1.1	19.5
17001 M.C.Z.	9.4	3.6	3.6	3.2	6.9	—	8.1	2.9	1.2	2.0	1.2	2.7	1.2	19.8
18894 M.C.Z.	—	—	3.5	3.5	7.4	1.7	9.1	3.0	1.2	2.3	1.4	3.0	1.3	21.5
average	9.5	3.7	3.7	3.5	6.8	1.6	8.2	2.9	1.2	2.1	1.2	2.7	1.2	19.8

Cranial Measurements. Continued

New Paris fossil—adult

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
5554 C.M.	8.9	3.6	3.8	4.1	5.9	1.5	7.9	2.9	1.3	2.0	1.2	2.9	1.2	18.5
5555 C.M.	—	—	4.1	—	—	—	8.5	—	1.2	1.9	1.2	2.7	1.2	18.0
5557 C.M.	—	—	—	—	6.0	1.5	8.2	2.5	1.2	1.9	1.0	2.4	1.0	—
5559 C.M.	—	—	3.6	—	6.5	1.5	8.1	2.9	1.2	2.2	1.3	2.7	1.2	19.5
5560 C.M.	—	—	3.8	3.6	6.3	1.3	—	2.9	1.3	1.9	1.2	—	—	19.0
5562 C.M.	—	—	4.2	3.9	6.7	1.5	7.9	2.9	1.2	2.1	1.2	2.4	1.2	18.5
5571 C.M.	—	—	3.9	4.0	6.2	1.4	—	—	—	—	—	—	—	—
5576 C.M.	—	—	—	—	7.2	—	—	2.9	1.2	1.9	1.3	—	—	—
5553 C.M.	—	—	4.0	3.8	6.0	1.6	7.8	—	—	—	—	—	—	19.0
average	8.9	3.6	3.9	3.9	6.4	1.5	8.1	2.8	1.2	2.0	1.2	2.6	1.2	18.7

Mandibular Measurements—*Microtus xanthognathus* (Leach)
Modern—immature

	1	2	3	4	5	6	7	8	9	10	11
5589 M.C.Z.	—	—	—	7.7	3.5	1.2	1.9	1.1	1.9	1.0	1.5
5590 M.C.Z.	18.5	—	—	7.0	3.1	1.1	1.6	.9	1.7	.9	1.2
18896 M.C.Z.	18.5	—	—	6.2	3.1	1.0	1.7	.9	1.3	.9	1.3
18897 M.C.Z.	18.0	—	—	6.3	3.1	1.2	1.6	1.0	1.5	.7	1.2
18939 M.C.Z.	18.0	—	—	6.9	3.4	1.2	1.7	1.1	1.9	1.0	1.2
4715 C.N.M.	17.0	4.3	5.2	6.8	3.1	1.2	1.7	1.0	1.7	1.0	1.2
average	18.0	4.3	5.2	6.8	3.2	1.2	1.7	1.0	1.7	.9	1.3

Mandibular Measurements. Continued

	1	2	3	4	5	6	7	8	9	10	11
Modern—adult											
1593 M.C.Z.	21.5	6.3	5.8	8.1	3.6	1.2	1.9	1.0	2.0	1.0	—
1601 M.C.Z.	—	—	—	7.7	3.3	1.2	2.1	1.2	1.9	1.1	1.6
5302 M.C.Z.	—	—	—	7.7	3.5	1.3	2.1	1.2	—	1.1	—
5307 M.C.Z.	—	—	—	7.4	3.4	1.2	1.7	1.0	1.7	1.1	1.4
5308 M.C.Z.	22.0	6.3	5.8	8.3	3.9	1.2	2.3	1.2	2.2	1.1	1.8
5584 M.C.Z.	20.0	7.3	—	7.3	3.6	1.1	1.9	1.0	1.2	.8	1.5
5585 M.C.Z.	21.0	—	—	7.7	3.6	1.1	1.9	1.0	1.9	.9	1.5
17001 M.C.Z.	21.0	—	—	7.6	3.5	1.3	2.1	1.2	2.1	1.1	1.5
18894 M.C.Z.	22.5	—	—	8.2	3.7	1.2	2.0	1.2	2.1	1.0	1.9
16004 A.M.N.H.	21.5	5.8	5.3	7.9	3.4	1.2	2.0	1.2	2.0	1.1	1.6
16006 A.M.N.H.	—	6.7	5.4	7.7	3.8	1.2	2.0	1.0	2.0	1.0	1.7
7702 U.S.N.M.	23.0	5.9	5.8	8.4	3.6	1.5	2.0	1.2	2.1	1.2	1.6
128330 U.S.N.M.	22.0	6.4	5.3	7.7	3.4	—	1.9	—	1.6	—	—
271710 U.S.N.M.	21.0	6.2	5.3	7.8	3.6	1.4	1.9	1.4	2.2	—	2.1
average	21.6	6.4	5.3	7.8	3.6	1.2	2.0	1.1	1.9	1.0	1.7
Mt. Solon—fossil	1	2	3	4	5	6	7	8	9	10	11
5561c C.M.	—	5.4	5.3	—	3.8	1.2	2.0	1.1	—	—	—
5561d C.M.	—	—	—	—	—	—	—	1.2	—	—	1.8
5561e C.M.	—	—	—	—	—	1.2	—	—	—	—	—

Mandibular Measurements—*Microtus xanthognathus* (Leach)
New Paris—fossil

	1	2	3	4	5	6	7	8	9	10	11
5534 C.M.	21.5	6.0	5.3	—	3.6	1.0	1.9	1.0	—	—	1.6
5535 C.M.	—	6.1	5.9	7.5	—	—	1.9	—	—	—	1.5
5536 C.M.	—	5.8	5.3	—	3.3	1.0	—	—	—	—	1.6
5537 C.M.	—	5.3	5.6	—	3.6	1.3	—	—	—	—	1.5
5538 C.M.	22.0	6.3	6.0	8.3	3.6	1.1	2.0	.8	1.9	1.0	—
5539 C.M.	—	—	—	—	—	—	1.9	1.2	—	—	1.5
5540 C.M.	19.0	5.1	5.3	7.2	3.4	—	1.9	—	1.7	—	—
5541 C.M.	21.0	6.1	5.6	8.0	3.5	—	1.9	—	1.9	—	1.8
5542 C.M.	21.5	5.4	5.6	7.9	—	—	—	—	—	—	1.7
5543 C.M.	—	5.5	5.3	—	3.6	1.1	1.9	1.2	—	—	—
5544 C.M.	21.0	5.8	5.8	7.6	3.5	1.0	1.9	1.1	—	—	1.6
5546 C.M.	18.8	5.1	5.6	7.1	3.3	1.1	1.9	1.1	—	—	1.2
5547 C.M.	19.5	—	—	7.7	—	—	1.7	1.1	1.9	1.0	1.5
5550 C.M.	—	—	—	—	—	—	—	—	—	—	1.5
5562 C.M.	—	5.8	5.8	—	3.6	—	1.9	—	—	—	1.6
5617 C.M.	—	5.6	5.7	—	3.5	1.1	2.1	1.2	—	—	1.6
average	20.5	5.7	5.6	7.7	3.5	1.1	1.9	1.1	1.9	1.0	1.6